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Title

Phylogeny, ecology and morphological evolution in the atelid cranium

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Abstract

Reconstructing evolutionary relationships of living and extinct primate groups requires reliable phylogenetic inference based on morphology, as DNA is rarely preserved in fossil specimens. Atelids (family Atelidae) are a monophyletic clade and one of the three major adaptive radiations of south and central American primates (platyrrhines), including the genera *Alouatta*, *Ateles*, *Brachyteles* and *Lagothrix*, and are diverse in morphology, body and brain size, locomotion, diet, social systems and behavioural ecology. Molecular phylogenetic relationships of the extant atelid genera are well resolved, yet morphological analyses often support alternative phylogenetic relationships to molecular data. We collected geometric morphometric data from the crania of atelid taxa for phylogenetic analysis of the cranium, cranial base and face, and tested the hypotheses that cranial data maintains a phylogenetic signal, cranial base morphology most closely reflects the atelid molecular phylogeny, and facial and overall cranial morphology are shaped by diet and have experienced greater homoplasy. All analyses supported genus monophyly, and facial morphology maintained a strong phylogenetic signal inferring the atelid molecular phylogeny and a sister relationship between *Brachyteles* and *Lagothrix*, whereas results from the cranial base and whole cranium supported *Ateles-Lagothrix* and/or *Alouatta-Brachyteles* clades reflecting homoplasy and ecological and dietary similarities. A phylogenetic signal in the atelid face is important for future studies integrating fossil taxa, and supports evidence that congruence between molecular and morphological phylogenetics in primates is module and clade-specific.

Keywords

Atelid, morphology, cranium, phylogeny, ecology, diet

Introduction

Phylogenetics is the study and reconstruction of evolutionary relationships between groups, and a phylogeny provides a framework and context within which to study the biology, and evolution, of organisms and traits they exhibit (Kitching et al. 1998, Schuh & Brower 2009, Philippe & Telford 2006, Fleagle 2013). Accurate phylogenetic analysis requires shared similarity in taxa to be inherited from a common ancestor, homology, rather than through convergent or parallel evolution, homoplasy (Lockwood & Fleagle 1999; Collard & Wood 2001; Hall 2007). Phylogenetic relationships are inferred using morphological, molecular or combined datasets; DNA sequencing has become prominent in systematics as it is cheap, fast and easy to use, generating large datasets that can be analysed with sophisticated statistical models to provide strongly supported, robust phylogenies. Despite the preference for molecular phylogenies, phylogenetic reconstruction using morphology is integral to understand the phylogenetic relationships and evolutionary history of extant and fossil species of primates, as DNA is rarely recovered from fossil groups (Jenner 2004, Wiens 2004).

Cranial morphology is used extensively for taxonomic and phylogenetic studies, and is formed by embryologically distinct but integrated regions including the face, vault and base, with the cranial base creating a platform for the brain to grow and a structure the face grows around (Lieberman *et al.* 2000a,b). Separate cranial regions have been proposed for the face, cranial vault and cranial base, with further subdivision into palate, temporal, orbit and zygomatic regions (Cheverud 1982; Cheverud 1995; Hallgrímsson *et al.* 2004; Goswami 2006). These regions, or modules, can be semi-autonomous with strong interaction between traits from the same module but weaker interaction between traits from different modules (Klingenberg 2008). Alternative biological factors and evolutionary forces will likely

differentially shape morphology and support alternative phylogenetic relationships for partially independent modules of the cranium (Wood & Lieberman 2001; Harvati & Weaver 2006a).

The cranial base region is strongly genetically determined and highly conserved due to its early ossification and role in multiple functional systems, and considered most likely to preserve a phylogenetic signal (Olson 1981; Lieberman *et al.* 1996; Lieberman 1997; Strait *et al.* 1997; Lockwood *et al.* 2004; Harvati & Weaver 2006a,b). In contrast, the facial skeleton is considered more developmentally plastic, highly influenced by epigenetic factors that mould its morphology, and less likely to maintain a reliable phylogenetic signal (Wood & Lieberman 2001; Harvati & Weaver 2006a; Smith *et al.* 2007). Several studies examined the phylogenetic signal of alternative modules in humans and Old World monkeys and found a strong phylogenetic signal in the cranial base (e.g. Harvati & Weaver 2006a,b, Smith *et al.* 2007, Cardini & Elton 2008).

Platyrrhines (Parvorder Platyrrhini) are monophyletic and speciose, including all primates native to Central and South America, and are important for studying morphological evolution due to their high diversity and variation, presence of unique adaptations, and an increasingly well-sampled fossil record. Molecular phylogenetic studies support three major platyrrhine clades: atelids, pitheciids and cebids (Schneider & Sampaio 2013). The atelids (family Atelidae) are a four-genus clade including the howler monkeys (*Alouatta*), spider monkeys (*Ateles*), woolly monkeys (*Lagothrix*) and miquis (*Brachyteles*), and a proposed fifth genus, *Oreonax* (Groves 2001), is a *Lagothrix* species (Matthews & Rosenberger 2008; Di Fiore *et al.* 2015; Ruiz-Garcia *et al.* 2015). Despite support for a trichotomy between *Ateles*, *Brachyteles* and *Lagothrix* based on several mitochondrial genes (Collins 2004), the majority

of platyrrhine and atelid phylogenetic studies based on single gene, multiple gene, and metagenomic approaches strongly support a *Brachyteles-Lagothrix* clade sister to *Ateles* with *Alouatta* basal-most (Schneider & Sampaio 2013; Jameson Kiesling *et al.* 2015; Di Fiore *et al.* 2015).

Alouatta has a wide distribution from northern Argentina to Mexico and extensive sympatry with other atelids, *Ateles* is mainly an Amazonian group but has dispersed into Central America and Mexico, *Lagothrix* is largely distributed in the western Amazon, and *Brachyteles* is isolated to the Atlantic coastal forest (Strier 1992; Rosenberger *et al.* 2009; Fleagle 2013). Atelids live in the upper forest canopy, have prehensile tails that support body weight during feeding and are used to varying degrees in locomotion, are the largest platyrrhines ranging in average body size from 10-11kg in *Brachyteles* to 6.5kg in *Alouatta*, and are diverse in social organisation, mating systems and life histories (Ford & Davis 1992; Hartwig *et al.* 1996; Kinzey 1997; Hartwig 2005; Di Fiore *et al.* 2011). *Lagothrix* and *Ateles* are predominantly frugivorous and *Alouatta* and *Brachyteles* are semi-folivorous or folivorous-frugivorous, with seasonal dietary flexibility in all groups (Norconk *et al.* 2009; Di Fiore *et al.* 2011; Rosenberger *et al.* 2011).

Alouatta is cranially distinct from other atelids in basicranium flexion and foramen magnum position, has airorhynch with a large face rotated onto the neurocranial axis and tilted upwards, a non-globular cranial vault, elongated muzzle, and a catarrhine-like configuration of the pterion (Rosenberger & Strier 1989; Cole 1995; Hartwig *et al.* 1996; Kinzey 1997; Bruner *et al.* 2004; Fleagle 2013). *Ateles*, *Lagothrix* and *Brachyteles* have larger relative brain sizes, share a rounded occipital and neurocranium, partially developed orbital torus and short basicranium (Rosenberger & Strier 1989; Hartwig *et al.* 1996; Kinzey 1997; Isler *et al.*

2008; Di Fiore *et al.* 2011; Hartwig *et al.* 2011; Rosenberger *et al.* 2011; Fleagle 2013).

Ateles and *Lagothrix* are frugivores with wide incisors and less molar shearing that probably reflect the ancestral phenotype, whereas *Alouatta* and *Brachyteles* share adaptations for folivory with buccal and lingual shearing respectively and narrow incisors (Rosenberger & Strier 1989; Rosenberger 1992; Anthony & Kay 1993).

Morphological analyses support multiple phylogenetic and functional relationships within the atelids. These include an *Alouatta-Brachyteles* and *Ateles-Lagothrix* dichotomy (Kay 1990; Horovitz & Meyer 1997; Horovitz *et al.* 1998), *Ateles* basal-most and *Alouatta-Brachyteles* sister to *Lagothrix* (Kay *et al.* 2008; Kay 2015), or *Alouatta* as the basal lineage and either *Ateles-Brachyteles* sister to *Lagothrix* (Rosenberger 1984; Rosenberger & Strier 1989; Hartwig 1993; Cole 1995), *Ateles-Lagothrix* sister to *Brachyteles* (Cole *et al.* 2002), or an unresolved trichotomy (Ford 1986). *Alouatta-Brachyteles* and *Ateles-Lagothrix* are respectively linked by folivory and frugivory, and a sister relationship between *Ateles* and *Brachyteles* maps to craniometric similarities and post-cranial adaptations associated with locomotion and brachiation (Rosenberger & Strier 1989; Hartwig 2005; Jones 2008).

The array of relationships recovered in morphology-based studies show there is a great deal to discover about atelid phenotypic evolution even if their phylogenetic relationships are considered ‘solved’ by molecular phylogenetics. We investigate the craniodental evolution of atelids, examining phylogenetic relationships inferred from 3-dimensional morphometric data incorporating four genera and 16 taxa of the atelid family. We compare phylogenetic inference from the whole cranium and modules of the face and cranial base, and consider results alongside the atelid molecular phylogeny, ecology and diet. We hypothesise there is a phylogenetic signal in the atelid cranium, that the cranial base will be more tightly genetically

controlled and closely reflect phylogeny, and that facial and overall cranial morphology will be more plastic and reflect dietary adaptations and ecology (Lieberman 1997; Strait *et al.* 1997; Wood & Lieberman 2001; Lockwood *et al.* 2004; Harvati & Weaver 2006a,b; Smith *et al.* 2007, Cardini & Elton 2008). We predict all phylogenetic analyses will support genus monophyly, cranial base morphology will most strongly reflect homology and support the molecular clade of *Brachyteles-Lagothrix*, whereas overall cranial and facial morphology will support *Ateles-Lagothrix* and *Alouatta-Brachyteles* clades reflecting dietary relationships and homoplasy.

Methods

We collected morphometric data from 327 pooled sex atelid specimens belonging to 16 taxa and 219 specimens from four outgroup taxa (Table 1) housed in the collections of the Natural History Museum London, Field Museum of Natural History Chicago, Museum für Naturkunde Berlin, Naturhistorisches Museum Wien, Smithsonian National Museum of Natural History Washington DC, Naturhistoriska Riksmuseet Stockholm and Anthropological Institute & Museum University of Zurich. Craniodental morphology was quantified for each specimen with sixty-three 3D anatomical landmarks that are points on an object/form that can be accurately located and have a clear, shared correspondence between specimens being studied (Klingenberg 2010) (Table 2 and Figure 1).

3D anatomical landmarks were analysed with geometric morphometric methods (GMM) using Generalised Procrustes Analysis, a mathematical superimposition process, that removes non-biological variation of scale, orientation and position, and generates new Procrustes shape residuals that measure and preserve the geometry of structures (Gower 1975; Rohlf & Slice 1990; Goodall 1991; Rohlf & Marcus 1993; Adams *et al.* 2004, Mitteroecker & Gunz 2009). GMM based on Procrustes superimposition are currently the most powerful and accurate methods to quantify and statistically analyse biological shape with the greatest power to test for differences in mean shape between populations, the highest accuracy in estimating mean shape, and the lowest error estimates (Rohlf 2000a,b, 2003).

Geometric morphometric analysis was completed in MorphoJ (Klingenberg 2011), and taxa mean shape described by geometric morphometric data were used to quantify morphological Euclidean distances separating pairs of taxa and were generated for all taxa combinations. Euclidean distances exist within linear Euclidean tangent space where multivariate analysis

of geometric morphometric data takes place and were measured as the square root of the sum of squared distances between two configurations of landmarks (Zelditch *et al.* 2004).

Morphological distances between mean shapes were calculated with an Excel macro and used for neighbor-joining distance-based phylogenetic analysis in the neighbor module of the Phylip software package (Felsenstein 2005). Distance-based phylogenetic methods are phylogenetic and use an outgroup to root the phylogenetic tree, with the exception of UPGMA (Unweighted Pair Group Method with Arithmetic Mean) (Cavalli-Sforza & Edwards 1967; Fitch & Margoliash 1967; Felsenstein 1984; Nixon & Carpenter 1993; Bryant 2001).

Neighbor-joining phylogenetic methods assume the distance between two taxa is equal to the distance between each respective group and a shared node, and use an agglomerative clustering algorithm, constructing a phylogenetic tree with a stepwise additive method that converts a star tree into a phylogeny using a divisive cluster algorithm (i.e. taxa are separated from each other into clades) that minimizes overall branch length (Saitou & Nei 1987; Kuhner & Felsenstein 1994; Desper & Gascuel 2005; Yang 2006). Neighbor-joining estimates a phylogenetic tree according to the smallest sum of branches, is statistically consistent, and infers the correct evolutionary tree when distances are accurate reflections of phylogeny (Nei & Kumar 2000; Mihaescu *et al.* 2009).

We report genus-level phylogenetic results as both consensus phylogenetic trees and in tables with statistical jack-knife node-support for groups congruent and incongruent with clades inferred from molecular data. Species-level phylogenetic relationships within genera are not reported for the sake of brevity and because the molecular phylogenetic results at those levels are not fully resolved or as strongly supported as the genus-level phylogeny, making

comparisons between morphological and molecular phylogenies difficult. Statistical node-support is presented as the number of times a clade inferred using a jack-knife procedure that excluded each anatomical landmark in turn and repeated Procrustes superimposition and subsequent phylogenetic analysis (Cardini & Elton 2008). For example, phylogenetic analysis of the face involves 15 landmarks, each landmark is removed and phylogenetic analysis repeated, and node support is 86.7% if four taxa form a clade in 13 of 15 analyses. The consensus module in Phylip was used to combine all phylogenetic analyses and compute node support (Felsenstein 2005).

Multiple outgroups were sampled to ensure phylogenetic results were robust. Geometric morphometric and distance-based phylogenetic analyses were repeated for atelids with four different outgroups including two Old World monkeys, the papionin *Macaca mulatta* and colobine *Colobus guereza*, and two New World monkeys, the pitheciid *Pithecia monachus* and cebine *Cebus apella*. We examined the phylogenetic signal of the whole cranium, described by 63 landmarks listed in Table 2, and subdivided the cranium into modules of the face (landmarks 1-15) and cranial base (landmarks 40-63). Previous studies of platyrrhines support craniodental modules including oral, nasal, orbit, zygomatic, cranial vault and cranial base regions (Cheverud 1995; Marroig & Cheverud 2001; Marroig *et al.* 2009; Porto *et al.* 2009; Shirai & Marroig 2010). However, we only repeated phylogenetic analyses of modules for the face and cranial base due to the lower number of landmarks that described the cranial vault and further anatomised regions, as general error for modules described by fewer landmarks becomes very high (Cardini & Elton 2008).

Results

Phylogenetic analysis of whole skull morphology (Tables 3 and 4) with *Macaca* and *Colobus* as outgroups inferred *Ateles-Lagothrix* sister to *Brachyteles* with over 95% clade support.

Analyses with *Cebus* as outgroup supported a dichotomy between *Ateles-Lagothrix* and *Alouatta-Brachyteles*, and with *Pithecia* as outgroup supported *Alouatta-Brachyteles* sister to *Lagothrix*, all clades with over 95% bootstrap support. All whole skull analyses provided 100% clade support for *Alouatta*, *Ateles* and *Lagothrix* monophyly, respectively.

All analyses of facial morphology (Tables 3 and 4) matched the atelid molecular phylogeny with *Brachyteles-Lagothrix* sister to *Ateles* and *Alouatta* basal-most. *Alouatta* and *Lagothrix* monophyly had 100% bootstrap support for all outgroups, and support for *Ateles* monophyly was between 70-80%. Support for the *Ateles-Lagothrix-Brachyteles* and *Lagothrix-Brachyteles* molecular clades were 100% for *Macaca* and *Pithecia* analyses, and between 65-75% for *Colobus* and *Cebus* analyses.

Phylogenetic analysis of the cranial base (Tables 3 and 4) with *Macaca*, *Cebus* and *Pithecia* as outgroup inferred a dichotomy between *Ateles-Lagothrix* and *Alouatta-Brachyteles*, supported with over 95% clade support. Cranial base results with *Colobus* as outgroup supported an *Ateles-Lagothrix* clade sister to *Brachyteles* with over 95% clade support. All cranial base results had 100% clade support for *Alouatta*, *Ateles* and *Lagothrix* monophyly.

Discussion

Phylogenetic analysis of atelid facial morphology recovered relationships congruent with molecular phylogenies, supporting our hypothesis there is a phylogenetic signal in atelid cranial morphology. The alternative cranial regions of the face and cranial base, described by separate, non-overlapping sets of landmarks (Table 2 and Figure 1), inferred alternative phylogenetic relationships as predicted. The presence of a phylogenetic signal in the atelid face rejected our hypothesis the face would be less phylogenetically informative than the cranial base, and runs counter to multiple theoretical and experimental primate studies that associated the cranial base with stronger genetic control and a conserved phylogenetic signal (Olson 1981; Lieberman *et al.* 1996; Strait *et al.* 1997; Lockwood *et al.* 2004; Harvati & Weaver 2006a; Cardini & Elton 2008). The phylogenetic signal in the atelid face highlights the region as integral to future phylogenetic analyses including fossil taxa, and reflects similarity of large, broad faces shared by *Lagothrix* and *Brachyteles* compared to the small and gracile head and face of *Ateles* (Rosenberger & Strier 1989; Cole 1995; Rosenberger *et al.* 2008). The basal-most atelid, *Alouatta*, has undergone extensive morphological diversification in the clade, evolving adaptations for howling, de-encephalized brains, and airorhynchy (Cole 1995; Kinzey 1997; Bruner *et al.* 2004; Isler *et al.* 2008; Di Fiore *et al.* 2011).

Weaker selective pressures on atelid facial morphology than for other cranial regions could maintain similarity by emphasising neutral, non-adaptive evolution correlating more closely with phylogeny. Natural selection rather than genetic drift is responsible for craniodental diversification in *Ateles*, *Brachyteles* and *Lagothrix* (Marroig & Cheverud 2004), and selection in other regions would need to be high to reconcile both scenarios. Atelids have greater morphological integration in the face than neural region (Marroig & Cheverud 2001),

and either a single adaptation could shift overall facial morphology and support a phylogenetic signal, or greater integration could make facial morphology less plastic and more resistant to change, conserving a phylogenetic signal.

The presence of a phylogenetic signal in primate facial morphology has also been found in hominoids, where correlations between molecular and morphological data were consistently strongest for facial morphology (von Cramon-Taubadel & Smith 2012), and evidence from cranial variation in baboons shows that masticatory stress and strain in the face does not lead to greater variability or make the region less informative for phylogenetic analyses (Roseman et al. 2010). Support for the genus-level molecular phylogeny in facial morphology, and higher genus monophyly in cranial base morphology, provides evidence from atelids that different elements of phylogenetic information are maintained dependent on the taxa examined and the macroevolutionary or taxonomic level studied (Harvati & Weaver 2006a). Our results reinforce the need to assess, on a case-by-case basis, the underlying processes influencing morphology and their impact on phylogenetic inference rather than seeking a single region that mirrors molecular phylogenies across all taxa (von Cramon Taubadel 2014).

Similarity inherited from a shared common ancestor, homology, and similarity due to convergent or parallel evolution not inherited from the last common ancestor, homoplasy, are fundamental to understanding atelid phylogenetics and evolution. It is likely that one of the *Ateles-Lagothrix* and *Alouatta-Brachyteles* clades supported by cranial base and whole skull analyses retained an ancestral phenotype and the other evolved similarity in parallel through homoplasy, complimenting convergent and parallel evolution identified in the platyrrhine and atelid post-cranium (Lockwood 1999; Jones 2008). The similarity of *Alouatta* and

Brachyteles may represent the ancestral atelid phenotype, but considering dental shearing in both taxa is a probable homoplastic adaptation linked to diet (Rosenberger & Strier 1989), the same evolutionary pressure could cause *Brachyteles* to converge on a derived *Alouatta* morphology from the phenotype of the more recent common ancestor with *Ateles* and *Lagothrix*. If *Brachyteles* diverged in cranial base morphology, and *Ateles* in facial morphology, *Lagothrix* would represent the least derived, ancestral atelid phenotype (Rosenberger & Strier 1989; Hartwig 1993).

Parallel evolution in extant atelids has precedence in the fossil record. *Cartelles coimbrafilhoi*, taxonomically reclassified from *Protopithecus brasiliensis* (Halenar & Rosenberger 2013), is similar to *Alouatta* with de-encephalization and a cranium modified for an enlarged vocal sac, but is frugivorous, evolved large body size estimated at 20-25kg, and has several post-cranial adaptations linked to suspensory locomotion and brachiation similar to *Ateles* and *Brachyteles* (Hartwig 1995; Hartwig & Cartelle 1996; Jones 2008; Hartwig *et al.* 2011, Halenar 2011a). The combination of being cranially specialized for howling and post-cranially adapted for brachiation would require major homoplasy, although the post-cranial locomotor behaviour of *Cartelles* has been challenged (Halenar 2011b, Halenar & Rosenberger 2013). Irrespective of the arguments around post-cranial adaptations, the presence of large body size in *Cartelles* requires convergence, as an additional atelid fossil taxa *Caipora bambuorum* is estimated to weigh around 20kg without the adaptations for howling (Cartelle & Hartwig 1996).

Homology and homoplasy can be identified using direct comparisons of molecular and morphological data, and by investigating trait evolution using a combination of phylogenetic, functional and developmental approaches (Lockwood 1999; Lockwood & Fleagle 1999,

Wake et al. 2011). The phylogenetic utility of traits depends on interpretation and scope, for example the presence of prehensile tails in atelids and *Cebus* can be considered a single character that evolved twice in platyrrhines through homoplasy, but sub-division into multiple tail characteristics show atelids share clear homology to the exclusion of *Cebus*, providing strong evidence of atelid monophyly prior to the advent of modern molecular phylogenetics (Rosenberger 1983, Lockwood 2007). Homoplasy is a biological reality providing invaluable data on phenotypic evolution and the interaction between environment, development and adaption, rather than a methodological error that distorts morphological studies (Lockwood 1999; Lockwood 2007; Wake et al. 2011).

Overall craniodental and cranial base morphology in atelids are predominantly shaped by homoplasy and ecological factors linked to diet, and seven out of eight of our phylogenetic analyses of the whole cranium and cranial base morphology inferred a sister relationship between *Ateles* and *Lagothrix* in agreement with several previous studies based on morphology (Kay 1990; Horovitz & Meyer 1997; Horovitz *et al.* 1998; Cole *et al.* 2002), and supported by dental similarities (Orlosky 1973; Hartwig 2005). *Ateles* and *Lagothrix* share a highly frugivorous diet and during mastication presumably experience a common response to similar mechanical properties and stress, and both exhibit a narrower, more gracile cranial base, dental arch and mandible compared to the more robust and folivorous *Brachyteles* and *Alouatta*. Despite the unique craniodental adaptations and diversification in *Alouatta*, five phylogenetic analyses supported a sister relationship between *Alouatta* and *Brachyteles*, four in a dichotomy with *Ateles-Lagothrix*, in agreement with past studies (Kay 1990; Horovitz & Meyer 1997; Horovitz *et al.* 1998). *Alouatta* and *Brachyteles* share dental adaptations for folivory and process a large proportion of leaves involving greater masticatory force, larger

mandibles and more robust cranial bases (Rosenberger & Strier 1989; Anthony & Kay 1993; Hartwig 1993; Norconk *et al.* 2009; Kay 2015).

Covariance in platyrrhine craniodental morphology appears dependent on dietary similarity, with diet and size evolution further linked to morphological diversification (Marroig & Cheverud 2001, 2004, 2005) which would explain the high support for an *Ateles-Lagothrix* clade in our phylogenetic analyses of the whole skull, although other work finds cranial shape differentiation is strongly linked to phylogeny and diet is less influential (Perez *et al.* 2011). This is augmented by body size diversification in modern Neotropical primate groups occurring very early in platyrrhine evolutionary history but without dietary niche differentiation as the primary cause (Aristide *et al.* 2015).

Several morphological studies supported an atelid clade with a sister relationship between *Ateles* and *Brachyteles* based on similarity in craniodental morphometry and shared locomotor behaviour and forelimb adaptations as advanced brachiators (Rosenberger 1984; Rosenberger & Strier 1989; Hartwig 1993; Cole 1995). Our phylogenetic analyses found no support for an *Ateles-Brachyteles* clade, with several post-cranial adaptations linked to locomotor behaviour likely homoplasies (Jones 2008). Differences in results to previous cranial morphometric studies (Hartwig 1993; Cole 1995) are partly methodological, with alternative methods used to quantify and statistically analyse morphology and greater emphasis in past studies on ontogeny and brain size evolution. The poor resolution of anatomical landmarks describing the cranial vault in this study could explain our lack of *Ateles-Brachyteles* clade support, as there is strong evidence for a shared increase in brain size (Cole 1995).

The development of molecular phylogenetics has provided an opportunity to re-examine morphology and challenge interpretations of trait evolution and the pattern of homology and homoplasy, leading to greater understanding of how clades and morphology evolve (Hartwig 2005). By analysing geometric morphometric data from the atelid cranium and considering inferred relationships in light of molecular phylogenetics, we identified a strong phylogenetic signal in facial morphology, whereas diet and ecology have driven evolution of whole skull and cranial base morphology. Developing a greater understanding of how morphology evolved in this clade offers a clear opportunity for taxonomic classification, reconstructing phylogenetic relationships and understanding the evolutionary forces that have shaped the morphology of extant atelids, the fossil taxa *Protopithecus* (Cartelles), *Caipora* and *Paralouatta*, and future fossils that are discovered (Rivero & Arredondo 1991, Hartwig & Cartelle 1996, Cartelle & Hartwig 1996, Horovitz & MacPhee 1999, Halenar & Rosenberger 2013).

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Figure 1 Anatomical landmarks on atelid *Lagothrix* specimen from anterior, lateral, posterior and basal perspectives (lines mark meeting points between bones). Numbers refer to landmarks listed in Table 2.

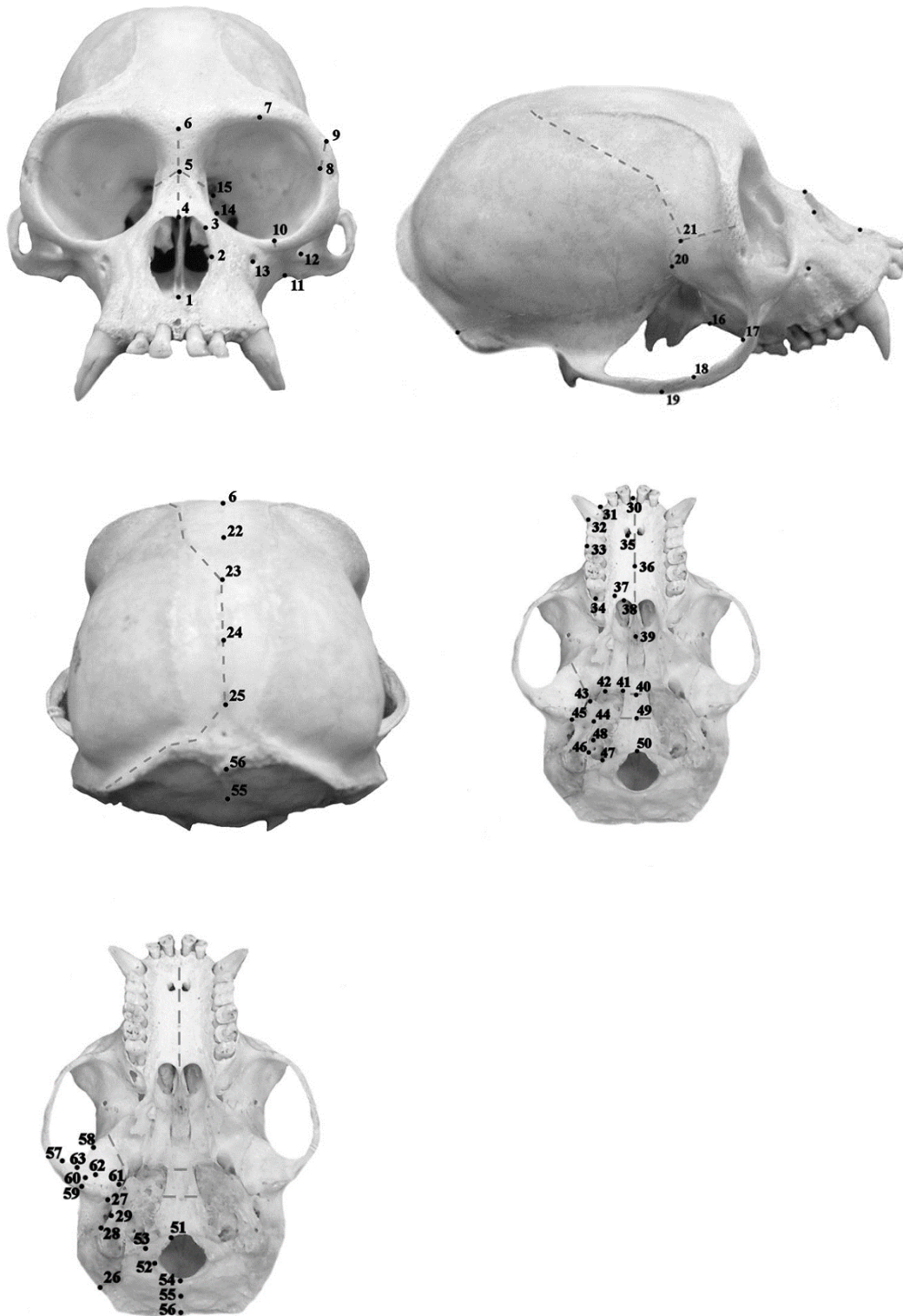


Table 1 Atelid and outgroup taxa sample sizes for pooled sex analyses

Taxa	Sample size
Ingroups	
<i>Alouatta belzebul</i>	20
<i>Alouatta caraya</i>	20
<i>Alouatta coibensis</i>	17
<i>Alouatta fusca</i>	18
<i>Alouatta palliata</i>	31
<i>Alouatta pigra</i>	18
<i>Alouatta seniculus</i>	32
<i>Ateles belzebuth</i>	21
<i>Ateles fusciceps</i>	20
<i>Ateles geoffroyi</i>	20
<i>Ateles paniscus</i>	19
<i>Brachyteles arachnoides</i>	12
<i>Lagothrix cana</i>	21
<i>Lagothrix lagothricha</i>	20
<i>Lagothrix lugens</i>	18
<i>Lagothrix poeppigii</i>	20
Outgroups	
<i>Colobus guereza</i>	21
<i>Macaca mulatta</i>	19
<i>Cebua apella</i>	152
<i>Pithecia monachus</i>	27

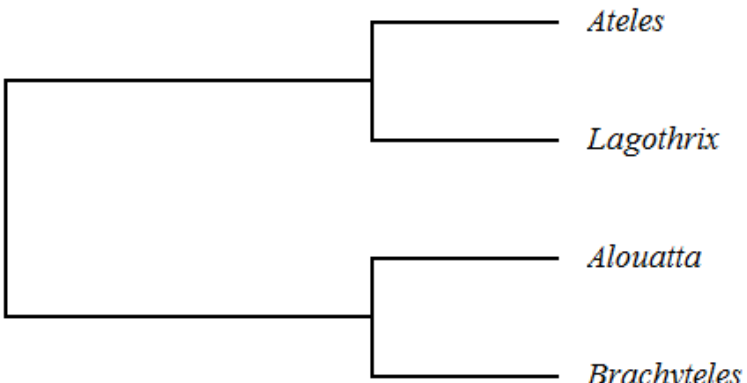
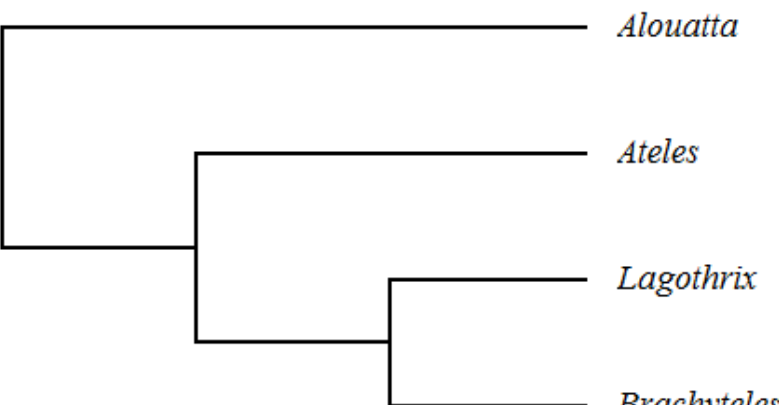
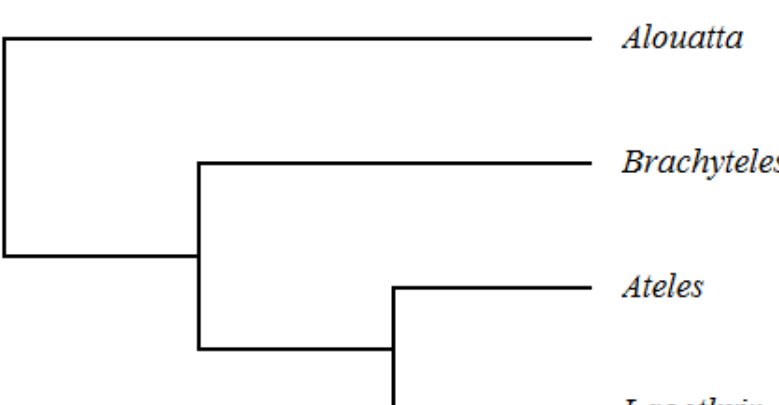
Table 2 List of anatomical landmarks

1. Piriform aperture nasospinale
2. Piriform aperture point of greatest width
3. Piriform aperture meeting of nasal and maxilla
4. Piriform aperture rhinion, most anterior midline
5. Nasion suture meeting of fronto nasals
6. Glabella midline point on frontal between supraorbital ridges
7. Supraorbital superior
8. Frontomolare orbitale
9. Frontomolare temporal
10. Zygo-max superior
11. Zygo-max inferior
12. Zygomatic foramen inferior
13. Infraorbital foramen inferior
14. Lacrimal duct fossa bottom
15. Optic foramen most medial
16. Upper posterior maxilla
17. Maximum point of curvature on upper zygomatic
18. Zygo-temp superior
19. Zygo-temp inferior
20. Meeting point of sphenoid and zygomatic
21. Meeting point of sphenoid, parietal and zygomatic process of temporal
22. Midpoint between glabella and bregma
23. Bregma

24. Midpoint between bregma and lambda
25. Lambda
26. Asterion
27. Auditory meatus anterior
28. Auditory meatus posterior
29. Auditory meatus inferior
30. Incisor I1 septum
31. Canine septum
32. Premolar P2 septum
33. Molar M1 septum
34. Midpoint of septum at end of dentition
35. Incisive foramen posterior
36. Meeting point of maxilla and palatine
37. Palatine foramen posterior/lateral
38. Max curvature of posterior edge of palatine
39. Nasal spine midpoint where wings split
40. Midpoint between basisphenoid and basioccipital
41. Petrous apex meeting point of petrous, basiosphenoid and basioccipital
42. Foramen lacerum
43. Meeting point of petrous, sphenoid and zygomatic process of temporal
44. Petrous greatest central projection
45. Stylomastoid foramen
46. Jugular foramen distal
47. Jugular foramen medial

48. Carotid foramen anterior
49. Midpoint between basion and basisphen-basioccipital
50. Basion anterior
51. Occipital condyle anterior apex
52. Occipital condyle posterior midpoint
53. Hypoglossal canal
54. Opisthion posterior
55. Midway between opisthion and inion
56. Inion
57. Greatest curvature on posterior zygomatic process of temporal
58. Temporal meeting point between sphenoid and zygomatic process of
59. Tip of post glenoid process
60. Deepest point within mandibular fossa
61. Articular eminence medial
62. Articular eminence midpoint
63. Articular eminence lateral

Table 3 Atelid consensus genus-level phylogenetic relationships inferred from morphometric data

Craniodental region	Outgroup(s)	Genera-level phylogeny inferred
Whole cranium Cranial base	<i>Cebus</i> <i>Macaca</i> <i>Cebus</i> <i>Pithecia</i>	 <pre> graph LR Root --- Node1 Node1 --- Ateles Node1 --- Node2 Node2 --- Lagothrix Node2 --- Node3 Node3 --- Alouatta Node3 --- Brachyteles </pre>
Face	<i>Cebus</i> <i>Pithecia</i> <i>Colobus</i> <i>Macaca</i>	 <pre> graph LR Root --- Node1 Node1 --- Alouatta Node1 --- Node2 Node2 --- Node3 Node3 --- Ateles Node3 --- Node4 Node4 --- Lagothrix Node4 --- Brachyteles </pre>
Whole cranium Cranial base	<i>Colobus</i> <i>Macaca</i> <i>Colobus</i>	 <pre> graph LR Root --- Node1 Node1 --- Alouatta Node1 --- Node2 Node2 --- Node3 Node3 --- Brachyteles Node3 --- Node4 Node4 --- Ateles Node4 --- Lagothrix </pre>

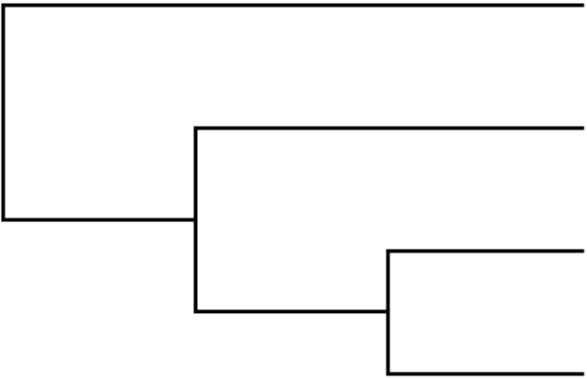
Whole cranium	<i>Pithecia</i>	 <pre> graph LR Root --- Node1 Node1 --- Ateles Node1 --- Node2 Node2 --- Lagothrix Node2 --- Node3 Node3 --- Alouatta Node3 --- Brachyteles </pre> <p><i>Ateles</i></p> <p><i>Lagothrix</i></p> <p><i>Alouatta</i></p> <p><i>Brachyteles</i></p>
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Table 4 Atelid jack-knife clade support for phylogenetic analysis of morphometric data

Whole cranium				
	Outgroup			
Molecular clade	<i>Colobus</i>	<i>Macaca</i>	<i>Cebus</i>	<i>Pithecia</i>
<i>Ateles</i>	100	100	100	100
<i>Lagothrix</i>	100	100	100	100
<i>Alouatta</i>	100	100	100	100
<i>Ateles-Lagothrix-Brachyteles</i>	100	98.4	<10	<10
<i>Brachyteles-Lagothrix</i>	<10	<10	<10	<10
Non-molecular clade				
<i>Ateles-Lagothrix</i>	100	100	100	<10
<i>Alouatta-Brachyteles</i>	<10	<10	100	98.4
<i>Alouatta-Brachyteles-Lagothrix</i>	<10	<10	<10	98.4
Face				
	Outgroup			
Molecular clades	<i>Colobus</i>	<i>Macaca</i>	<i>Cebus</i>	<i>Pithecia</i>
<i>Ateles</i>	80	80	73.3	80
<i>Lagothrix</i>	100	100	100	100
<i>Alouatta</i>	100	100	100	100
<i>Ateles-Lagothrix-Brachyteles</i>	66.7	100	73.3	100
<i>Brachyteles-Lagothrix</i>	86.6	100	93.3	100
Non-molecular clade				
<i>Ateles-Lagothrix-Alouatta</i>	13.3	<10	<10	<10

<i>Ateles-Alouatta</i>	<10	<10	26.7	<10
<i>Ateles belzebuth-Ateles paniscus- Alouatta</i>	<10	<10	26.7	<10
<i>Ateles geoffroyi- Ateles fusciceps-Lagothrix-Brachyteles</i>	<10	<10	<10	20
Cranial base				
	Outgroup			
Molecular clades	<i>Colobus</i>	<i>Macaca</i>	<i>Cebus</i>	<i>Pithecia</i>
<i>Ateles</i>	100	100	100	100
<i>Lagothrix</i>	100	100	100	100
<i>Alouatta</i>	100	100	100	100
<i>Ateles-Lagothrix-Brachyteles</i>	95.8	<10	<10	<10
<i>Brachyteles-Lagothrix</i>	<10	<10	<10	<10
Non-molecular clade				
<i>Ateles-Lagothrix</i>	100	100	95.8	100
<i>Alouatta-Brachyteles</i>	<10	95.8	100	100

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